

POPULATION STRUCTURE AND ECOLOGICAL EFFECTS OF THE CRAYFISH *PACIFASTACUS LENIUSCULUS* IN CASTLE LAKE, CALIFORNIA

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ABSTRACT.—The recent appearance of the “California crayfish,” *Pacifastacus leniusculus*, in Castle Lake, California, and interest in its potential impacts on the lake ecosystem provided motivation for a study of the population structure and habitat use of this species and its effects on aquatic macrophytes. Mark-recapture studies indicated that the total number of adult (3+ yr or older) crayfish in the lake was ca 10,100 individuals, yielding an estimate of lakewide crayfish density in preferred crayfish habitats of 0.13 adults m⁻². Using mean body mass of individuals, we estimated that ambient biomass density was 5.9 g m⁻². Length-weight relationships determined for captured individuals were sex dependent, with males having greater body mass for a given carapace length. Length-frequency and weight-frequency diagrams indicated that *P. leniusculus* reaches larger sizes in Castle Lake than do populations of *P. leniusculus* in ultraoligotrophic Lake Tahoe. Population-wide, males were significantly larger in both carapace length and body mass than females. We also examined sex dependence of interhabitat differences in crayfish body size by comparing animals trapped in rocky areas with those from areas with macrophytes and soft sediments. No significant differences in overall body size were found between habitats, but a significant habitat-sex interaction term occurred because the sex-dependent size differences were more pronounced in sediment than in rocky areas. Enclosure and enclosure experiments indicated that crayfish had large but differential impacts on Castle Lake macrophyte species, as the abundance of two of the dominant species (*Chara* sp., *Potamogeton richardsonii*) declined in the presence of crayfish and, in one case, increased in enclosures. These effects occurred via both consumptive and nonconsumptive mechanisms. These studies indicate that an expanding population of *P. leniusculus* in Castle Lake may be producing sizable impacts on the littoral zone habitat.

Key words: crayfish, herbivory, macrophytes, *Pacifastacus leniusculus*.

Littoral zones are important to the dynamics of lake ecosystems (Wetzel 1983, Carpenter and Lodge 1986). Vascular plant communities (macrophytes) are particularly important in the littoral zone, providing food resources for herbivores, attachment substrata for periphyton, and cover for both predators and prey. Macrophytes are also particularly important in fueling detritus food chains (Wetzel 1983). Traditionally, studies have generally emphasized the influence of physical (e.g., light availability or wave action; Spence 1982) and chemical (inorganic carbon; Sand-Jensen 1978) factors in regulating littoral zone macrophyte communities; as a result, biotic interactions, particularly herbivory, have been considered less important (Gregory 1983, Wetzel 1983).

However, recent experimental studies indicate that invertebrate and vertebrate herbivores can have large impacts on macrophytes and that herbivory impacts vary for different

macrophyte species (Lodge 1991). Crayfish may be particularly important in influencing the dynamics of littoral zone plant communities because of their diverse feeding modes; crayfish may act as predators (consuming other littoral zone invertebrates), as herbivores, or as detritivores. Past studies of crayfish impacts on macrophytes indicate that their effects occur directly (via both consumptive and nonconsumptive mortality; Lodge and Lorman 1987) as well as indirectly via predation on other potential herbivores (Hanson et al. 1990). However, only a few of the 11 genera and 300 named species and subspecies of crayfish in North America (Bouchard 1978) have been studied with respect to their potential impacts on littoral zone vegetation.

The “California crayfish,” *Pacifastacus leniusculus*, is a member of family Astacidae and includes three subspecies with a range that encompasses northern California and much of the Pacific Northwest (Miller 1960).

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Abrahamsson and Goldman (1970) suggested that *P. leniusculus*, introduced to Lake Tahoe at the turn of the century, were important in determining the distribution of macrophyte communities at depths less than 50 m. Flint and Goldman (1975) subsequently supported this suggestion experimentally, showing that *P. leniusculus* controlled *Myriophyllum* at shallow depths. Flint and Goldman also demonstrated that low levels of crayfish grazing enhanced primary productivity by attached algae.

In 1988 researchers observed individuals of *P. leniusculus* in the littoral zone of Castle Lake, where it had been unrecorded previously during nearly 30 years of ecological research (Beatty 1968, Swift 1968, Neame 1975, Carlton 1982, Paulsen 1987, Hagley 1988). Therefore, in the summer of 1990 we began studies designed to evaluate population size and structure, habitat utilization, and potential effects on macrophyte communities of *P. leniusculus* in this subalpine lake.

MATERIALS AND METHODS

Study Site

Castle Lake is a relatively small (20 ha) but deep (35 m maximum depth) subalpine lake located in the Siskiyou Mountains of northern California (Siskiyou County), USA (41° 13' N, 122° 22' W). The main basin of the lake is relatively steep sided, but the lake contains an extensive shallow (<4 m) shelf on its northeast side. Bottom substrates are diverse and include steep-sided rock faces and boulders in the vicinity of the lake's cirque face, coarse particulate-dominated sediments in the vicinity of forested slopes, and flocculent, low-density organic sediments that cover most of the bottom of the main basin below depths of 10 m as well as much of the shallow shelf. According to recent work of Hagley (1988), the most abundant macrophyte species of Castle Lake are *Isoetes occidentalis* (Henders.), *Chara* sp., and *Potamogeton* sp. (*P. richardsonii* [(Benn.) Rydb.] is dominant but *P. granineus* [L.] is also present.)

Population Estimates

Estimates of crayfish population abundance were made via the multiple-recapture Schnabel method (Schnabel 1938), with cap-

turing, marking, releasing, and resampling of animals occurring at biweekly intervals from July through mid-September 1990. Animals were captured using cylindrical nylon-mesh traps with funneled entrances and baited with dead fish. Traps were set overnight in shallow waters (<10 m) in all areas of the lake in late afternoon or early evening and retrieved in early morning. To estimate depth distribution of crayfish in the Castle Lake littoral zone, on five occasions we established transect trap lines across the depth contours of the lake to determine the maximum depths at which crayfish could be found; each transect sample consisted of 15 traps placed at 10-m intervals along a nylon line. These extended to a depth of ca 25–30 m. Sex, carapace length, and wet weight of each animal were recorded. Animals were also classified with respect to areas from which they were obtained, i.e., rocky bottoms vs. those with organic sediments. All large animals (generally >35 mm carapace length [CL], age 3+ yr according to Abrahamsson and Goldman [1970], although similarly sized individuals in Castle Lake may be younger than those growing in ultraoligotrophic Lake Tahoe) were given unique marks via cauterization of the carapace (Abrahamsson 1965) and returned to the lake. We rarely captured recently moulted crayfish, indicating that the majority of moulting had occurred prior to our sampling period. Thus, our results are not likely to be complicated by potential changes in trapability in response to moulting events. A total of 750 animals were eventually marked during the sampling period.

Enclosure/Enclosure Studies of the Effects of *P. leniusculus* on Macrophytes

To examine potential ecological effects of crayfish on the macrophyte communities of Castle Lake, we performed an 8-wk enclosure/enclosure experiment. Cages consisted of 1 × 1 × 1-m wood-framed cages covered with 0.9-cm mesh nylon netting on sides and top. Replicate ($n = 4$) enclosures received either one or three adult male crayfish (50–52 mm carapace length, ca 47 g body weight), equivalent to densities of 47 g m⁻² and 141 g m⁻², respectively. Adult crayfish were used because earlier studies suggested that smaller crayfish tend to be more carnivorous than herbivorous, while adults are usually primarily herbivorous

(Abrahamsson 1966). Logistical constraints on the size of enclosures we could use meant that enclosure densities were likely higher than ambient crayfish densities (see Results). Thus, we also decided to maintain four enclosures that received no additions of crayfish and were inspected to ensure that no animals had been enclosed. Results of enclosure treatments thus are critical in assessing whether potential herbivore impacts detected in enclosures with artificially high animal densities are likely to be operating in the lake itself. Support for the hypothesis that crayfish are exerting an impact on macrophytes in the lake itself would come not only from depressed biomass of macrophytes in enclosure treatments but more importantly from increases in macrophyte biomass in enclosures where macrophytes are protected from ambient grazing intensity. When each enclosure or enclosure was positioned, a control section of equal area was also delineated to be sampled at the end of the experiment to enhance the power of statistical analyses. Without paired control areas, high site-to-site variation in local macrophyte abundance might overwhelm treatment effects even if treatments substantially altered local macrophyte abundance. Thus, a total of eight enclosures and four exclosures, each with a paired control area, were monitored.

Cages, with control areas, were placed along the 3–5-m contour interval within vegetated areas of the lake. Cages were checked at weekly intervals via scuba, and crayfish were added to enclosures from which animals had escaped (this happened twice); no crayfish were observed inside exclosures. At the end of the 8-wk period, the above-sediment portions of all submersed macrophytes in each cage and control area were harvested, sorted by species, drained, and weighed to the nearest gram.

RESULTS AND DISCUSSION

The estimated population size of adult *P. leniusculus* (i.e., individuals ≥ 3 yr) in Castle Lake obtained using the Schnabel method was $10,100 \pm 23$ (SD) individuals. Our trap transects across depth contours in the lake indicated that crayfish did not generally inhabit bottom areas below 10 m, as at these depths the bottom is dominated by soft, flocculent sediments. Likewise, animals were rarely caught

in traps placed in much of the shallow shelf area of the lake, which is also dominated by soft sediments lacking macrophyte development. Thus, we then estimated the total amount of crayfish habitat as the total bottom area shallower than 10 m ($117,000 \text{ m}^2$) minus the estimated area of the shallow shelf dominated by soft sediments (ca $42,400 \text{ m}^2$), yielding a total habitat area of ca $74,600 \text{ m}^2$. Thus, average crayfish densities in Castle Lake were approximately $0.13 \text{ adults m}^{-2}$. This estimate is somewhat lower than, for example, the estimates of densities of *P. leniusculus* made by scuba census and trapping efficiency in ultraligotrophic Lake Tahoe ($0.16\text{--}5.85 \text{ adults m}^{-2}$) and oligotrophic Donner Lake ($0.23\text{--}0.44 \text{ adults m}^{-2}$) reported by Abrahamsson and Goldman (1970), Flint and Goldman (1977), and Goldman and Rundquist (1977). Some of this discrepancy may reflect differences in methodology (mark-recapture, which focused only on adults, vs. scuba census or trapping efficiency methods, which included juvenile animals). In addition, our estimate is likely to be on the low side as we conservatively included bottom areas down to 10 m although our transect data indicate that a majority of catches were made at depths shallower than 5 m. Therefore densities in the habitat areas predominantly used by *P. leniusculus* in Castle Lake are likely higher and likely approach the lower end of the range reported for Lake Tahoe (ca $0.2 \text{ adults m}^{-2}$).

By stratifying the population estimates based on relative catches in different parts of the lake, we estimated populations of 8000 individuals in rocky-bottomed areas of the lake and 2100 in macrophyte-dominated areas. Average body mass (male and female) of sampled crayfish was 45.6 g, and therefore areal biomass of crayfish in Castle Lake was 5.9 g m^{-2} . The sex ratio for animals in all catches was 0.90 (female:male).

Length and wet-weight measurements were made on approximately 1188 animals during the course of the sampling season. Length-weight relationships differed significantly for males and females (based on confidence limits on the slopes of the length-weight relationships), with males having greater body mass for a given carapace length, especially at larger sizes (Fig. 1). This may reflect the fact that male chelae undergo allometric growth during ontogeny, while female

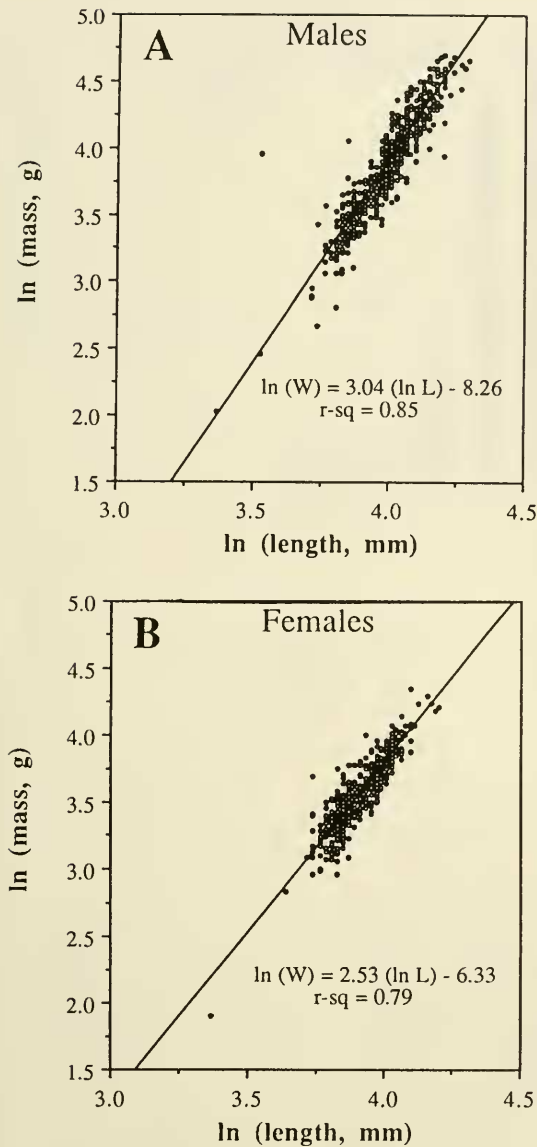


Fig. 1. Length-wet weight relationships for male (A) and female (B) crayfish. Allometric relationships fit to the data are given.

chela grow isometrically (Mason 1975). In addition, males were on the whole larger in carapace length (and body mass) than females ($P < .05$ based on a t test; Fig. 2), possibly reflecting the fact that females must necessarily invest substantial portions of their energy budgets in reproductive output. The size frequency distribution (Fig. 2) was quite broad, with largest individuals reaching 70^+ mm CL. This contrasts with the results of the studies by Abrahamsson and Goldman (1970) and

Flint (1975) of *P. leniusculus* in ultraoligotrophic Lake Tahoe, where the largest animals observed were around 55 mm CL. Without more detailed sampling and cohort analyses it is not possible to determine whether this difference reflects faster growth rates or longer life span in Castle Lake relative to Lake Tahoe.

We also used ANOVA to compare male and female sizes in different habitat categories (rocky vs. sediment/macrophyte areas; Fig. 3). While there was no significant main effect of habitat type on crayfish body size, there was a significant habitat \times sex interaction, as male body size in sediment/macrophyte areas was higher than in rocky areas, with the opposite being true for female crayfish. It is important to note that baited traps are biased in favor of large males (Brown and Brewis 1978); thus, interpretation of data on sex-dependent differences in body size between habitats is complicated by the possibility that trap bias operates differently at different locations. Bearing this in mind, the patterns illustrated in Figure 3 may reflect interacting influences of burrow availability in different habitats and size- and sex-dependent dominance patterns between individual crayfish. Behavioral studies of *P. leniusculus* are limited, but the study of Momot and Leering (1986) indicated that, within sexes, large *P. leniusculus* are dominant over small but that, for animals of the same size, females dominate over males. Given this suggestion and our lack of knowledge about general burrow availability in different bottom types in Castle Lake, we can only speculate about the factors contributing to observed sex-dependent differences in body size between habitat types. It is possible, for example, that general burrow shortages in sediment regions cause these regions to be dominated by the largest (and therefore most dominant) male crayfish able to successfully defend the limited number of available burrows, resulting in a larger mean body size for males in sediment areas. However, the observation that the opposite pattern was true for females (females tended to be larger in rocky areas than in sediment areas) suggests that simple dominance patterns and general burrow shortages are insufficient to explain these data, as it is possible, for example, that the quality of available burrows may be different for females than for males. Experimental studies of burrow choice

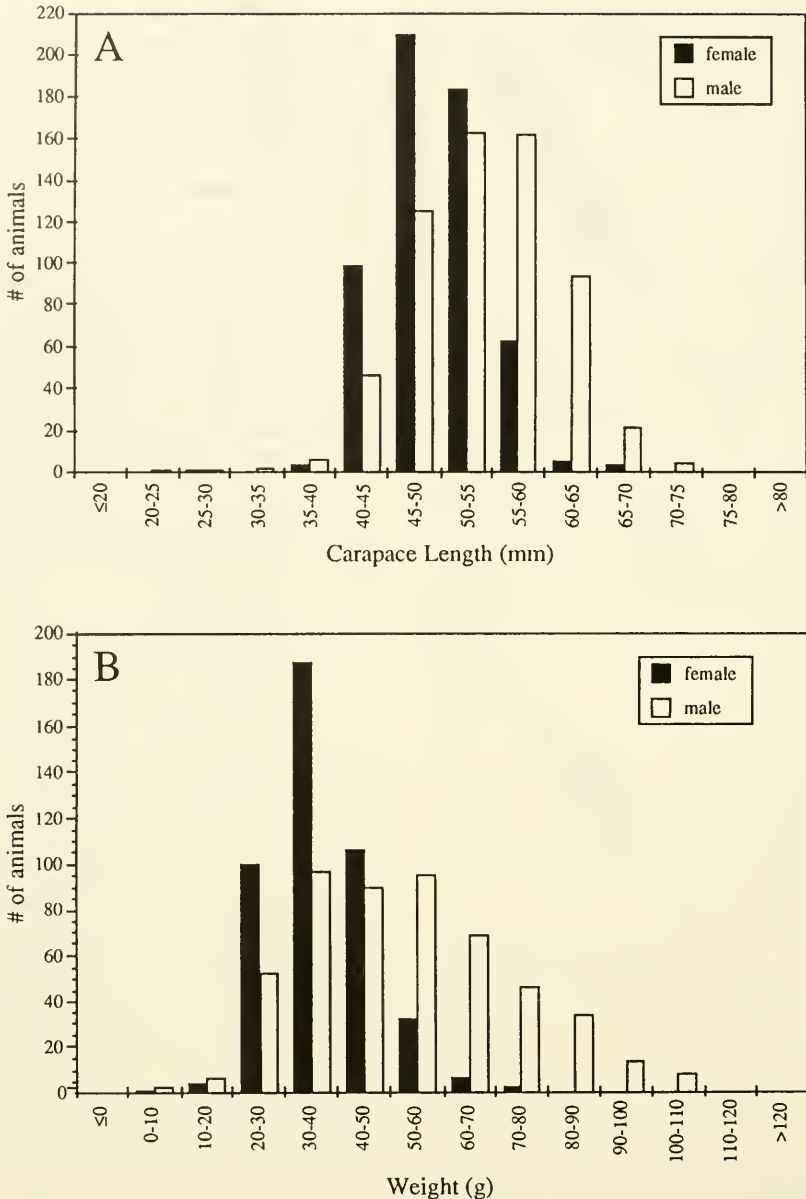


Fig. 2. Length-frequency (A) and weight-frequency (B) diagrams for male and female crayfish. Males were significantly ($P < .05$) larger and heavier than females.

and defense and aggressive displacement in different habitats, as well as the sex-dependence of these phenomena, are needed to elaborate on these possibilities.

Our enclosure/exclosure experiment indicates that *P. leniusculus* exerts substantial grazing pressure on the aquatic macrophytes of Castle Lake, as both total biomass and biomass of certain species responded to the presence or absence of crayfish (Fig. 4). However,

densities of crayfish used in the experimental enclosures (one or three adult male crayfish per square-meter enclosure) exceeded our estimates of ambient densities of adult crayfish in the lake (ca 0.15–0.20 crayfish m^{-2}) by more than fivefold. High densities of crayfish in enclosures were the necessary result of having to construct enclosures of manageable size that would not disturb, or be disturbed by, other human users of the lake. The observation

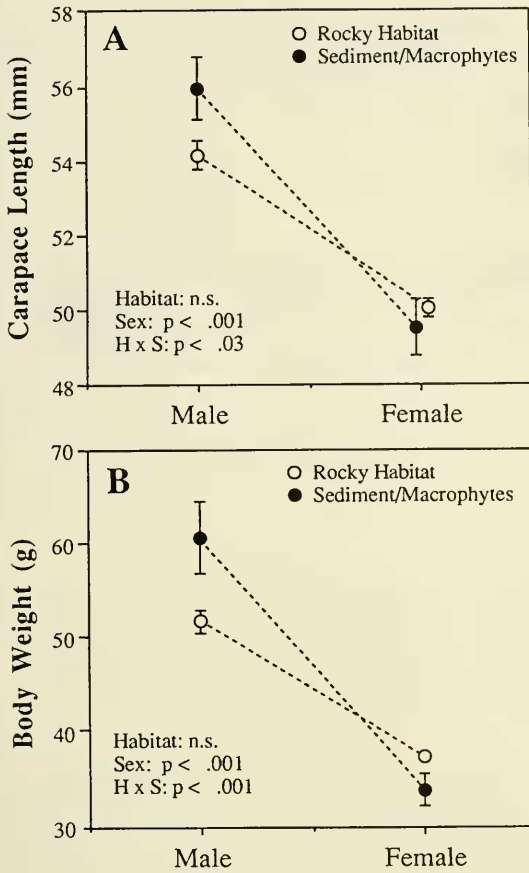


Fig. 3. Body size of male and female crayfish in different habitat types: A, carapace length; B, body weight. Analysis of variance indicated no significant main effect of habitat on animal size, but there was a significant habitat-sex interaction ($P < .001$), reflecting a pronounced difference between habitats in males but an opposite, and lesser, difference for females. Error bars represent ± 1 SE for each mean.

that crayfish impacts did not increase in three- vs. one-crayfish treatments suggests that the artificially high crayfish densities in enclosures created unrealistic intensities of herbivory. Thus, the potential exists that reductions in macrophytes relative to control areas reflect these artificially high levels of crayfish and that crayfish grazing at ambient levels is inconsequential for macrophytes. However, this conclusion is not supported by the observation that macrophyte biomass increased greatly in enclosures, which prevent ambient crayfish grazing, relative to control areas exposed to crayfish. *Chara* biomass increased in the enclosure treatment by a factor even greater than its decline in the enclosure treat-

ments, consistent with our prediction that, if crayfish grazing is important under natural lake conditions, macrophyte biomass should increase strongly when ambient grazers are excluded. We also observed that *Chara* canopies in experimental enclosures were more branched, taller, and more open than *Chara* stands in both the crayfish enclosures and the lake itself, suggesting that crayfish grazing is important in the natural lake condition, a conclusion supported by our observation during nighttime scuba dives that most of the observable crayfish could be found feeding on the *Chara* beds.

The impact of *P. leniusculus* on macrophytes was clearly species dependent. No effect of either enclosures or enclosures was observed for *Isoetes*, a pteridiophyte with relatively tough leaves arranged in a basal rosette. No statistically significant impacts were detected for *Potamogeton* either. However, these results are misleading, as they are largely an artifact of the general scarcity of *Potamogeton* in the Castle Lake littoral zone. This scarcity resulted in a poor representation of *Potamogeton* among experimental treatments (only one enclosure and a single one-crayfish enclosure had *Potamogeton* initially and in the adjacent control area). In fact, in all four cases where *Potamogeton* occurred in enclosures with crayfish, abundance was reduced to zero as crayfish snipped off the single-stemmed plants at the base. This example of nonconsumptive mortality is similar to that observed by Lodge and Lorman (1987) for *Orconectes rusticus* feeding on *Megalodonta beckii* and *Vallisneria americana*. The impact of such whole-plant mortality is undoubtedly more extreme in its impact than partial consumption of individual plant parts and may account for the general scarcity of *Potamogeton* in Castle Lake. The low impact of *P. leniusculus* on *Isoetes* may reflect the low potential food values of this species. Hagley (1988) reports a high C:N ratio for *Isoetes* in Castle Lake (ca 14–18:1 by weight vs. 10–11:1 for *Chara* and *Potamogeton* vegetative shoots); low C:N ratios in plant materials are generally considered indicative of nutritionally superior foods for a wide variety of herbivores (Mattson 1980, Crawley 1983).

Biomass of the macroalga *Chara* changed significantly in both enclosures and enclosures. This response reflects consumptive grazing by crayfish, as we never saw severed *Chara* "stems" inside crayfish enclosures. The

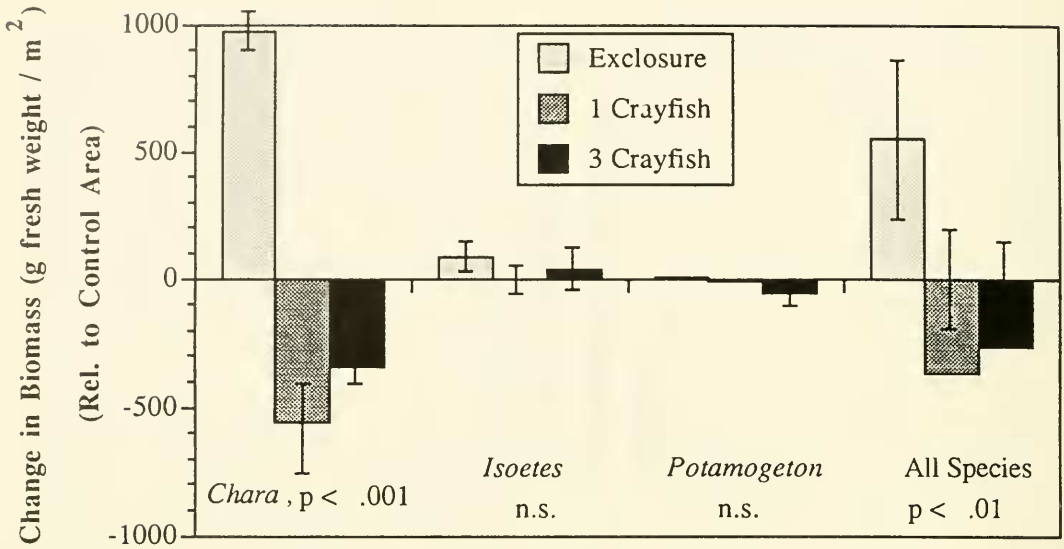


Fig. 4. Results of crayfish enclosure/exclosure experiments. Analysis of variance indicated the presence of crayfish had significant effects on total macrophyte abundance ($P < .01$) and on *Chara* ($P < .001$). Although *Potamogeton* was nonconsumptively eliminated in all enclosures in which it occurred with crayfish, no statistically significant effect was observed for *Potamogeton*, largely a result of poor representation of this species among experimental units. *Isoetes* was unaffected by crayfish. Error bars represent ± 1 SE for each mean. Error bars are missing for the enclosure and one-crayfish treatments for *Potamogeton* because *Potamogeton* was present in both treatment and control areas in only one replicate pair for these treatments.

substantial and rapid increase in *Chara* biomass in enclosures indicates that crayfish potentially regulate the natural abundance of *Chara* in Castle Lake; high *Chara* growth rates may permit it to persist in the face of this consumption. Overall distributions of these macrophytes are consistent with the differential impacts of crayfish just described: *Isoetes* dominates bottom areas with large crayfish populations while *Potamogeton* is confined to sediment-dominated littoral zone areas where crayfish abundance is lowest. In sum, our observations of the abilities of *Pacifastacus leniusculus* to differentially regulate macrophyte species in this lake lend further support to the conclusions of Lodge (1991) that macrophytes are actively engaged in aquatic food webs via direct consumption by herbivores, in addition to their role as contributors to detrital-based trophic pathways.

Given the potential influences of crayfish-induced mortality on Castle Lake macrophytes demonstrated by the cage experiments, it would be of interest to know the history of the *P. leniusculus* population in this system. Previous thorough investigations of the Castle Lake littoral zone do not report any crayfish. However, crayfish carapaces were observed in

the lake as early as 1986 (E. Marzolf personal communication), and a substantial population was verified during gill net studies of Castle Lake rainbow trout begun in 1988. This places the date of potential introduction of crayfish in the mid-1980s, as a considerable amount of littoral zone research occurred in Castle Lake in the early 1980s with no report of crayfish (e.g., Paulsen 1987, Hagley 1988). In the absence of a more thorough evaluation of present-day species composition, spatial distribution, and biomass development of Castle Lake macrophytes, it is not possible to evaluate whether these assemblages changed during the period between the macrophyte studies of Hagley (1988) prior to crayfish introduction and 1990 when our study was performed. However, given that invasions of new species into unoccupied habitats are often explosive, population densities of *P. leniusculus* in Castle Lake may increase even further and approach those densities actually used in our experimental enclosures; this possibility is supported by recent (1992–93) crayfish trapping, which indicates that catch-per-unit-effort may have increased by a factor of 2–3 since our 1990 study (J. J. Elser personal observation). Thus, our experimental studies likely yield

some insights into the impacts on macrophytes of further population development of *P. leniusculus*, providing an additional illustration of the effects of invading species on aquatic ecosystems.

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